

HEADSTANDERS OF THE NEOTROPICAL
ANOSTOMID GENUS *ABRAMITES*
(PISCES: CHARACIFORMES: ANOSTOMIDAE)

Richard P. Vari and Ann M. Williams

Abstract.—The anostomid characiform genus *Abramites* Fowler (1906) is revised and two species are recognized. *Abramites eques* (Steindachner, 1878) occurs only in the Río Magdalena basin of Colombia. *Abramites hypselonotus* (Günther, 1868) is distributed through the Río Orinoco, Río Amazonas, and the Río Paraguay-lower Río Paraná systems. The two species can be distinguished via differences in pigmentation, meristics, and morphometrics. *Leporinus solaris* Holmberg (1887), *Abramites microcephalus* Norman (1926), *Abramites ternetzi* Norman (1926) and *Leporinus nigripinnis* Meinken (1935) are placed as synonyms of *Abramites hypselonotus* (Günther). The genus is characterized by its deep body, postpelvic median keel, increased anal-fin ray count, and perhaps by a unique autogenous ossification on the dorsomedial surface of the fourth infrapharyngobranchial. A key is provided to the species of *Abramites*.

The genus *Abramites* comprises a small group of distinctive anostomid characiforms whose common aquarium name of “headstanders” derives from their habit of resting in life with the body at a distinct angle with the head down (see Géry 1977: 177 for life photos showing this trait). *Abramites* species occur in the Río Magdalena system of trans-Andean northwestern South America, and in the Río Orinoco, Río Amazonas and the Río Paraguay and lower Río Paraná systems of the cis-Andean slope of the continent. The two species we recognize as valid, *Abramites hypselonotus* (Günther, 1868) and *A. eques* (Steindachner, 1878), were originally described as members of the large anostomid genus *Leporinus*. Fowler (1906:331) advanced *Abramites* for *A. hypselonotus*, citing the longer anal-fin base in that species as a character distinguishing it from the remainder of *Leporinus*. Eigenmann (1920a:31, 1920b: 16, 1923:117) expanded *Abramites* by adding *Leporinus eques* Steindachner of the Magdalena system in Colombia, a practice

followed by Norman (1926:92–94). Borodin (1929:287), apparently unaware of Eigenmann’s and Norman’s publications, independently noted that *Leporinus eques* Steindachner was closely aligned to *L. hypselonotus*. Although Borodin discussed two additional characters diagnostic for *Abramites* relative to *Leporinus* (sensu stricto), he considered the two taxa to be congeneric. The synonymy of *Abramites* into *Leporinus* was continued by some authors (e.g., Eigenmann and Allen 1942:305 and 308), but most researchers have followed Fowler in recognizing a distinct *Abramites* for this readily distinguishable group of anostomid fishes.

Although the overall body form readily delimits the genus, the number of recognizable species of *Abramites* has not previously been analyzed in depth. Böhlke (1958:101–105) presented evidence for the synonymy of *Abramites microcephalus* Norman into *A. hypselonotus* (Günther). The other nominal cis-Andean species have not been the subject of thorough systematic studies. Dif-

ferent authors have inconsistently recognized some of the nominal forms at the specific or subspecific levels and have differed on the number of recognizable forms. The resolution of these problems was historically hampered by the limited samples of *Abramites* specimens in systematic collections. Recent collecting activities in the Amazon, Orinoco, and La Plata basins have provided additional specimens from all three systems, making possible a resolution of the remaining species-level questions.

Methods and materials.—Measurements were made with dial calipers and data recorded to tenths of a millimeter. Counts of total vertebrae were taken from radiographs and include the four vertebrae of the Weberian apparatus. The fused PU_1+U_1 is considered a single element. The numbers in parentheses following a particular vertebral count are the numbers of radiographed specimens with that count. In species descriptions, subunits of the head are presented as a proportion of head length (HL). Head length itself and measurements of body parts are given as proportions of standard length (SL). In the counts of median and pelvic fins, unbranched fin-rays are indicated by lower case Roman numerals, and branched fin-rays are indicated by Arabic numerals. The observed range of each count and measurement is presented first, followed by the value of the holotype or lectotype when available, in square brackets. The "Material examined" section of each species account follows the arrangement in Vari (1984).

Specimens examined for this study are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); British Museum (Natural History), London (BMNH); California Academy of Sciences, San Francisco (CAS); Colección Ictiológica del Museo de La Plata (CIMLP), La Plata; Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum, Los

Angeles (LACM); Museo de Biología, Universidad Central de Venezuela, Caracas (MBUCV); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Muséum d'Histoire Naturelle, Geneva (MHNG); Museo de Zoología da Universidade de São Paulo (MZUSP); Naturhistoriska Riksmuseet, Stockholm (NRM); Naturhistorisches Museum Wien, Vienna (NMW); University of Michigan, Museum of Zoology, Ann Arbor (UMMZ); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Abramites Fowler

Abramites Fowler, 1906:331, type *Leporinus hypselonotus* Günther, by original designation.

Diagnosis.—*Abramites* is a distinctive group of anostomid characiforms, which attain an adult body size of 200 mm SL (Dahl 1971:112). The genus is characterized by a deep, laterally-compressed body, a distinct postpelvic median keel extending between the base of the pelvic fin and the anus, and a high anal-fin ray count. A unique autogenous ossification on the dorsomedial surface of the cartilaginous fourth infrapharyngobranchial may also characterize the genus (see below).

Rayed dorsal-fin rays i,10–11 or ii,9,i or ii,9–11 or iii,10 (when three unbranched rays present, first very small); anal-fin rays i,12 or ii,10–12 or iii,11–14 (when three unbranched rays present, first very small); pectoral-fin rays 13 to 15; pelvic-fin rays i,7–8 or i,7,i (rare); principal caudal fin rays 10+9; adipose dorsal fin always present. Pored lateral line scales from supracleithrum to hypural joint 33 to 36 (33 rare); 4 to 6 pored scales beyond hypural joint on base of caudal fin. Number of scales in a transverse series from origin of dorsal fin to lateral line 6 to 7½ (6 and 7½ rare); number of scales in a transverse series from origin of anal fin

to lateral line 5 to 6½ (5 rare). Four teeth on each side of lower jaw and three teeth on premaxilla. No teeth on maxilla. Pharyngeal dentition bicuspidate, limited to fifth ceratobranchial and fifth upper pharyngeal tooth plate.

Remarks. — The two species recognized in this study, *Abramites hypselonotus* (Günther) and *A. eques* (Steindachner), were originally described as a part of the much larger genus *Leporinus*. Fowler (1906:331) advanced *Abramites* for *A. hypselonotus* in light of the longer anal-fin base in that species relative to the remainder of *Leporinus*. Eigenmann (1907:769) stated that “The name is not admissible” due to the absence of a distinct gap in the anal-fin ray counts of *Abramites* versus the remaining *Leporinus* species. He returned *hypselonotus* to *Leporinus* (Eigenmann and Kennedy 1907: 512; Eigenmann, McAtee, and Ward 1907: 125; Eigenmann 1909:323 and 344, 1910: 426). Later without comment, Eigenmann (1920a:31, 1920b:16, 1923:117) both recognized *Abramites* and expanded the genus to include *Leporinus eques* Steindachner. Although Norman (1926) noted some additional diagnostic characters for *Abramites*, Borodin (1929:287) preferred not to recognize the genus because he believed that a subdivision of *Leporinus* should be the result of a more inclusive study. With a few exceptions (Eigenmann and Allen 1942:308, Schultz 1944:268), subsequent authors have nonetheless recognized *Abramites*. Overall phylogenetic relationships within the Anostomidae remain unresolved other than for the subfamily Anostominae examined by Winterbottom (1980). The absence of information on the phyletic history of *Abramites*, *Leporinus* and associated genera makes it impossible unequivocally to determine whether the recognition of *Abramites* would make *Leporinus* non-monophyletic. If *Abramites* represents a specialized subunit within *Leporinus*, then the recognition of both genera would result in a non-monophyletic *Leporinus*. There is, how-

ever, no phylogenetic analysis that indicates this is the situation, or even evidence that a broadly defined *Leporinus* including *Abramites* constitutes a natural assemblage. In the absence of such information and in light of a series of derived characters unique to *Abramites*, we prefer to recognize the genus.

The most obvious of the series of evidently derived characters delimiting *Abramites* is the increase in the greatest body depth relative to all other anostomids, which typically have fusiform or relatively shallow bodies. Correlated with that character is the possession of a postpelvic median keel unique to *Abramites* among anostomids. Fowler first proposed the genus (1906:331) due to its “larger anal basis,” presumably referring to the higher number of branched anal-fin rays relative to the condition in other anostomids. That distinction is valid for the vast majority of *Abramites* and *Leporinus* (*sensu stricto*). Ten branched anal-fin rays, nonetheless, occur both in rare individuals of *Abramites hypselonotus* and some specimens of the anostomid *Anostomoides laticeps* Eigenmann (Eigenmann 1912:299, Géry 1977:178).

An additional character possibly synapomorphic for *Abramites* is found in the dorsal portion of the gill arches. Anostomids have an extensive fourth infrapharyngo-branchial (PB₄) with a reduced, posterolaterally angled fourth upper pharyngeal tooth plate (UP₄) (see Vari 1983: fig. 20). In that bauplan the medial and dorsal surfaces of the cartilaginous PB₄ lack any bony covering. *Abramites hypselonotus* has a discrete autogenous ossification in the posterodorsal lateral surface of PB₄ (Fig. 1). The ossification is very small in a 62 mm SL cleared and stained specimen, but very prominent in a 97 mm SL individual. Such an autogenous ossification is not found in the remaining examined anostomid genera (*Anostomus*, *Gnathodolus*, *Laemolyta*, *Leporellus*, *Rhytiodus*, *Schizodon*, and *Synaptaemus*) and its possession is consequently

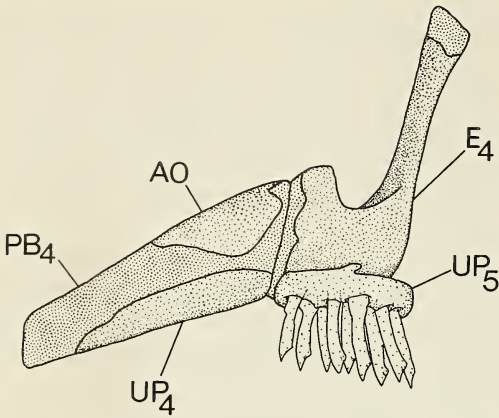


Fig. 1. *Abramites hypselonotus*, USNM 164036, fourth and fifth upper pharyngeal tooth plates (UP₄, UP₅), fourth infrapharyngobranchial (PB₄), fourth epibranchial (E₄) and autogenous ossification of fourth infrapharyngobranchial (AO), right side, medial view.

considered derived. The absence of material of *Abramites eques* suitable for clearing and staining prevents examination of the condition in that species. As such, we can only tentatively suggest that the autogenous ossification is a synapomorphy for the genus.

The form of upper jaw dentition suggested by Myers (1950:193) as distinctive for *Abramites* has not, on further examination, proved to be unique to the genus among anostomids. Borodin (1929:287) stated that "the gill membranes . . . are only feebly attached in *Leporinus hypselonotus*" contrary to the firm attachment in other *Leporinus* species. We have been unable to find any difference in the condition of the gill membrane attachment between *Abramites* and *Leporinus* (*sensu stricto*).

Key to the species of
Abramites Fowler

- 1. Branched anal-fin rays 13 or 14. Five transverse bars on body; anterior-most bar under dorsal fin
.....*A. eques* (Steindachner)
- Branched anal-fin rays 10 to 12. Eight transverse bars on body; bars

distributed between nape and rear of caudal peduncle
..... *A. hypselonotus* (Günther)

Abramites hypselonotus (Günther)
Figs. 2–6, Table 1

Leporinus hypselonotus Günther, 1868a: 480, type locality: Upper Amazon, Xeberos (=Jeberos), Peru.—Günther, 1868b: 244, pl. XXII, Peru, Xeberos.—Cope, 1878:690 Peru, Pebas.—Steindachner, 1882:12, Venezuela, Ciudad Bolivar.—Eigenmann and Eigenmann, 1891:51, citation.—Eigenmann and Kennedy, 1903: 512, Asuncion or Matto (=Mato) Grosso.—Eigenmann, McAtee and Ward, 1907:125, Paraguay, Puerto Max.—Eigenmann, 1909:323,344, Orinoco, Amazon and Paraguay basins.—Eigenmann, 1910:426, citation.—Bertoni, 1914:10, Paraguay.—Borodin, 1929:287, pl. 17, Brazil, Manacapuru.—Bertoni, 1939:54, Paraguay.—Eigenmann and Allen, 1942: 308, Peru, Iquitos.—Schultz, 1944:268, citation.

Leporinus Solarii Holmberg, 1887:222, type locality: Argentina, Río Paraná, Misiones.—Holmberg, 1891:187, Argentina, Río Paraná, Misiones.

Leporinus eques, Boulenger, 1896:34, misidentification of *L. hypselonotus*, Brazil, Descalvados and San Luis (=São Luís), Matto (=Mato) Grosso.—Eigenmann, 1909:344, Amazon and Paraguay basins.

Abramites hypselonotus, Fowler, 1906:331, designated as type species of *Abramites*.—Norman, 1926:94, in key.—Fowler, 1945:129, literature compilation.—Myers, 1950:193, Peru, Pevas.—Böhlke, 1958:101, Ecuador, Chickerota and Río Pucuno, *Abramites microcephalus* Norman placed as a synonym.—Ringuelet and Aramburu, 1961:37, Argentina.—Géry, 1964:35, Peru, Iquitos.—Ovchynnyk, 1968:249, Ecuador, Río Bobonaza and Río Pucuno.—Mago-Leccia, 1970:75,



Fig. 2. *Abramites hypselonotus*, BMNH 1977.3.10:146–149, 33.0 mm SL; Peru, Loreto, vicinity of Iquitos.

Venezuela.—Fowler, 1975:108, citation.—Géry, 1977:175, in key.

Leporinus solarii, Eigenmann, 1909:349, lower Río Paraná and Río La Plata.—Eigenmann, 1910:426, Río de La Plata.—Pozzi, 1945:258, Argentina.—Meinken, 1937:74, middle Río Paraná, *L. nigripinnis* Meinken placed into synonymy.

Abramites microcephalus Norman, 1926:92 and 94, type locality: near the mouth of the River Amazon.—Pozzi, 1945:258, Argentina.—Fowler, 1950:250, literature compilation.—Böhlke, 1958:101, placed as synonym of *Leporinus hypselonotus* Günther.—Fowler, 1975:108, citation.

Abramites ternetzi Norman, 1926:93–94, type locality: Brazil, Matto (=Mato) Grosso, São Luís and Descalvados.—Ringuet, 1975:72, upper Río Paraguay.—Fowler, 1975:108, citation.

Leporinus salarii: Borodin, 1929:288, as a possible synonym of *L. hypselonotus*, specific name misspelled.

Leporinus nigripinnis Meinken, 1935:193, fig. 1, type locality: Argentina, Corrientes.—Meinken, 1937:74, *L. nigripinnis* placed as synonym of *L. solarii* Holmberg.—Pozzi, 1945:258, Argentina.

Abramites solarii, Ringuelet, Aramburu and Alonso de Aramburu, 1967:213, fig. 9A, Argentina, Santa Fe, Laguna Setúbal, and Corrientes, Isla Apipé Grande.—Ringuet, 1975:61, Río Paraná and Río Paraguay.—Bleher, 1986:72, Paraguay, Río Pilcomayo.

Abramites eques, Fernández-Yépez, 1950:116, Venezuela, Río Salinas.—Mago-Leccia, 1970:75, Venezuela.

Abramites hypselonotus ternetzi, Géry, 1977:175, Río Paraguay basin.

Abramites hypselonotus hypselonotus, Géry, 1977:75, Amazon and Orinoco basins.

Diagnosis.—The possession of 10 to 12 branched anal-fin rays and eight bars of irregular shape on the body between the nape and the caudal peduncle distinguishes *Abramites hypselonotus* from *A. eques*, which has 13 or 14 rays and 5 bars extending from under the dorsal fin to the caudal peduncle. The two species also differ in the relative length of the postorbital portion of the head and interorbital width (Table 1).

Description.—Morphometrics of the lectotype and other specimens of the species given in Table 1. Body compressed laterally;

Table 1.—Morphometrics of *Abramites hypselonotus* and *A. eques*: A, *Abramites hypselonotus*, lectotype; B, *A. microcephalus*, holotype; C, *A. ternetzi*, lectotype; D, Range for all examined specimens of *A. hypselonotus*; E, Lectotype of *A. eques*; F, Range for lectotype and paralectotypes of *A. eques*. Standard length expressed in mm; measurements 1 to 10 are proportions of standard length; 11 to 15 are proportions of head length.

	A	B	C	D	E	F
Standard Length	98.9	101.7	54.3	40.0–123.4	138.8	106.7–163.7
1. Greatest body depth	0.39	0.42	0.42	0.34–0.47	0.36	0.34–0.36
2. Snout to dorsal-fin origin	0.49	0.49	0.52	0.46–0.53	0.45	0.45–0.48
3. Snout to anal-fin origin	0.77	0.80	0.82	0.74–0.84	0.73	0.73–0.77
4. Snout to pelvic-fin origin	0.49	0.48	0.51	0.46–0.52	0.46	0.45–0.48
5. Snout to anus	—	0.77	0.77	0.73–0.79	0.71	0.71–0.75
6. Origin of hypural fin to hypural joint	0.58	0.62	0.61	0.56–0.63	0.61	0.57–0.61
7. Least depth of caudal peduncle	0.12	0.12	0.13	0.11–0.13	0.12	0.12
8. Pectoral-fin length	0.22	0.21	—	0.19–0.24	0.20	0.19–0.21
9. Pelvic-fin length	0.21	0.19	—	0.18–0.24	0.23	0.21–0.23
10. Head length	0.26	0.23	0.26	0.23–0.29	0.23	0.23–0.25
11. Snout length	0.28	0.31	0.30	0.27–0.34	0.30	0.29–0.32
12. Orbital diameter	0.26	0.28	0.33	0.25–0.33	0.29	0.25–0.29
13. Postorbital head length	0.38	0.40	0.35	0.34–0.42	0.43	0.43–0.46
14. Interorbital width	—	0.39	0.35	0.34–0.43	0.45	0.43–0.46
15. Gape width	—	0.22	0.19	0.18–0.23	0.20	0.18–0.20

deep, more so in larger individuals. Greatest body depth at origin of dorsal fin. Dorsal profile of head straight in specimens under 45 mm SL, becoming somewhat concave above orbit in larger specimens. Dorsal profile of body very slightly convex to insertion of dorsal fin in individuals under 50 mm SL, curvature increasing with size, largest individuals with a distinct predorsal hump. Predorsal region with an obtuse median ridge. Body profile straight, posteroventrally slanted at base of dorsal fin, straight or slightly convex from insertion of posterior-most dorsal-fin ray to caudal peduncle. Ventral profile of head nearly straight in juveniles, slightly convex in larger specimens. Prepelvic profile of body becoming increasingly convex in larger specimens. Postpelvic body profile smoothly rounded to caudal peduncle. Prepelvic region transversely rounded; postpelvic region with a trenchant median keel terminating posteriorly at anus.

Head pointed in profile, more so in larger specimens, interorbital region transversely

convex. Upper and lower jaws equal. Anterior and posterior nostrils of each side distinctly separated, anterior tubular, posterior an oblique slit.

Lower jaw with four teeth on each side. Two medial teeth with inner surfaces spoon-shaped and a strong medial cusp grading into a smaller lateral cusp. Third tooth much smaller with cusps less distinct. Lateral tooth small, peg-like, not readily visible except in cleared and stained specimens, lacking in smaller individuals. Upper jaw with three teeth on premaxilla, none on maxilla. Two medial teeth with inner surfaces spoon-shaped. Distal portion of medial tooth triangular with a smaller medial cusp; middle tooth triangular; lateral tooth distinctly smaller with a straight distal margin. Gill membranes tightly attached to urohyal.

Scales cycloid, firm. Pored lateral line scales between supracleithrum and hypural joint 33 to 36 (33 only in the one available specimen from the Rio Araguaia) [35]; 4 to 6 pored lateral line scales extending beyond hypural joint onto base of caudal fin; canals



Fig. 3. *Abramites hypselonotus*, UMMZ 207433, 43.8 mm SL; Paraguay, Misiones, Rio Parana.

in lateral line scales straight or slightly divergent. Scales in transverse series from lateral line to origin of dorsal fin 6 to $7\frac{1}{2}$ (6 and $7\frac{1}{2}$ rare) [$6\frac{1}{2}$]. Scales in transverse series from lateral line to origin of anal fin 5 to $6\frac{1}{2}$ (5 rare) [$5\frac{1}{2}$].

Rayed dorsal fin obtusely pointed, last unbranched and first and second branched rays longest. Dorsal-fin rays i, 10–11 or ii, 9, i or ii, 9–11 or iii, 10 (when three unbranched rays present, first very small; i, 10–11, ii, 9, i and iii, 10 less common) [ii, 10]. Adipose fin of moderate size, unscaled. Anal-fin margin slightly convex to slightly concave. Anal-fin rays i, 12 or ii, 10–12 or iii, 11–12 (when three unbranched rays present, first very small) [ii, 11]. Pectoral-fin obtusely pointed, extending about two-thirds to three-quarters distance to vertical through insertion of pelvic fin. Pectoral-fin rays 13 to 15. Pelvic fin obtusely pointed, extending approximately one-half to two-thirds distance to anus. Pelvic-fin rays i, 7–8 or i, 7, i [i, 8]. Caudal-fin forked, unscaled. Principal caudal-fin rays 10+9.

Vertebrae 37(12), 38(8) [38].

Coloration in preservative.—Overall ground coloration of specimens fixed in formalin and lacking guanine on scales tan, more silvery in individuals retaining gua-

nine. Head with band of dark pigmentation on snout from anterior surface of lower lip to anterior margin of orbit. A posterodorsally angled band from rear margin of orbit to above opercle. Middorsal portion of head dark. Body with eight vertical or slightly posteroventrally aligned bars; bars sometimes incomplete or broken vertically. First bar extends from nape to behind pectoral-fin insertion. Second bar from middle of predorsal region to posterior one-third of prepelvic region. Third bar developed ventrally to varying degrees; extending to pelvic-fin insertion in some individuals. Fourth bar very prominent, running between dorsal-fin base and region of pelvic fin. Fifth bar a distinct band (Fig. 2), or subdivided into dorsal and ventral sections (Figs. 3, 4), or vertically divided ventrally (Fig. 5). Sixth bar terminating ventrally at anterior portion of anal fin, anteriorly expanded midlaterally in individuals with horizontally subdivided fifth bar (Figs. 3, 4). Seventh bar on caudal peduncle. Eighth bar at base of caudal-fin rays, crescent shaped, with prominent dark spot at base of middle caudal-fin rays in juveniles (Fig. 2). Dorsal fin with anterior rays and basal portion of remaining rays darkly pigmented. Adipose fin darkly pigmented basally and sometimes along dorsal

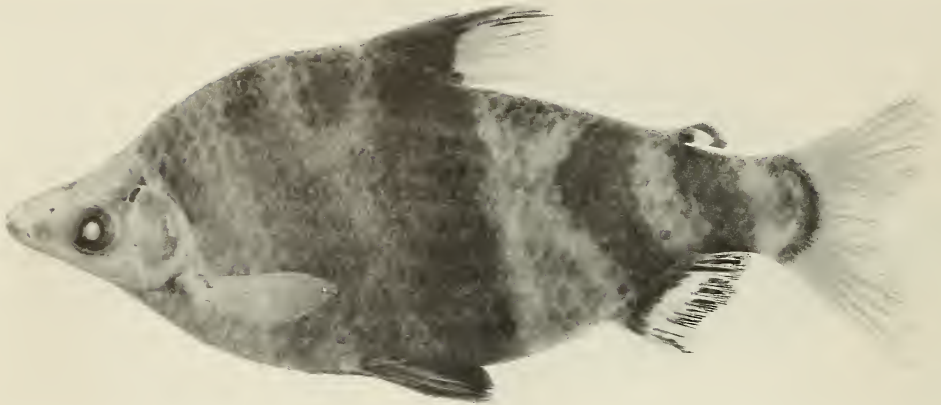


Fig. 4. *Abramites hypselonotus*, MZUSP 27721, 88.7 mm SL; Brazil, Mato Grosso do Sul, Rio Taquari.

margin. Anal fin ranging from darkly pigmented, through mottled, to clear. Pelvic fin darkly pigmented. Pectoral and caudal fins hyaline. See also "Remarks" for discussion of geographic variation in pigmentation.

Common names.—Peru: San Pedrito (Ortega and Vari 1986); Paraguay: Per-dofolha (Eigenmann and Kennedy 1903); Venezuela: Picúo (Mago-Leccia 1970); Argentina: Jikii (Ringuelet, Aramburu and Aramburu 1967).

Remarks.—Species of the genus *Abramites* have a very distinctive body form and pigmentation pattern and demonstrate relatively little morphological variation. Nonetheless, *A. hypselonotus* has four junior synonyms, one described from the Amazon basin and three from the Paraguay-lower Paraná system. In part this may be a consequence of the pronounced ontogenetic increase in body depth in the species, compounded by geographic variation in pigmentation.

Norman (1926:92) described *Abramites microcephalus* on the basis of a single specimen originating "near the mouth of the River Amazon." That nominal form was purportedly distinguished from *A. hypselonotus* Günther by differences in the relative length of the head and pelvic fins. Böhlke

(1958:101–103) noted that these characters did not adequately delimit the two nominal forms and thought it "best to consider *microcephalus* a synonym of *hypselonotus*." Our studies on a much larger series of Amazonian specimens than were available to Böhlke have shown a continuum in all characters between the nominal forms (Table 1) and support Böhlke's placement of *microcephalus* into the synonymy of *hypselonotus*.

The three nominal *Abramites* species from the Paraguay-lower Paraná system are *Leporinus solarii* Holmberg (1887), *Abramites ternetzi* Norman (1926) and *Leporinus nigripinnis* Meinken (1935). The proliferation of names for La Plata basin *Abramites* is in large part a consequence of Norman and Meinken's apparent lack of knowledge of *Leporinus solarii* Holmberg. Norman, in his key to *Abramites*, did not mention *solarii*, and a similar lapse characterized Meinken's (1935) publication. Once Meinken learned of the existence of Holmberg's species, he placed his nominal species, *Leporinus nigripinnis*, as a synonym of *L. solarii* (Meinken 1937). More recently Géry (1977) has drawn attention to the similarities between the three nominal La Plata basin *Abramites* species. Although neither the type series of *Leporinus solarii* nor that of *L. nigripinnis*



Fig. 5. *Abramites hypselonotus*, MCZ 59420, 98.6 mm SL; Ecuador, Rio Punino, above Coca.

is evidently extant, the data and figures in the original descriptions together with an examination of the lectotype and paralectotypes of *Abramites ternetzi*, leave no doubt as to the conspecificity of the three nominal *Abramites* species from the La Plata basin.

Specimens of *Abramites* from the Orinoco and Amazon basins and those from the Paraguay-lower Paraná system are indistinguishable on the basis of examined meristic and morphometric features (Table 1), although there are some differences in the "typical" pigmentation patterns between the populations. Individuals from the Amazon and Orinoco basins typically have unpigmented anal fins (Fig. 5) whereas samples from the La Plata basin usually have the fin pigmented (Fig. 4). However, individuals with varying amounts of dark pigmentation on the anal fin are found in low numbers in the Amazon populations, and individuals with little or no anal-fin pigmentation occur in Paraguay-Paraná samples. Similarly, the third and fifth vertical bars are typically vertically incomplete or broken in individuals from the Paraguay-Paraná system (Figs. 3, 4) contrary to their usual full development in Amazonian and Orinocan specimens (Figs. 2, 5). Nonetheless, Amazonian basin individuals with pat-

terns similar to those of the La Plata basin form are encountered in moderate numbers. As a consequence, no discrete difference in pigmentation exists to discriminate the nominal *solarii* of the La Plata basin from Amazonian *hypselonotus*.

In light of the lack of any known characters, pigmentary, meristic or morphometric, to delimit the nominal forms from the different cis-Andean basins, they are considered conspecific. A single species, *Abramites hypselonotus* (Günther), ranging from the Orinoco to Paraná basins, is recognized with four synonyms: *Leporinus Solarii* Holmberg, *L. nigripinnis* Meinken, *Abramites microcephalus* Norman, and *A. ternetzi* Norman.

Leporinus hypselonotus was described by Günther from three specimens now in relatively poor condition. The individual in the best condition (BMNH 1867.6.13:40, approx. 100 mm SL) is designated as the lectotype, and the two remaining syntypes (BMNH 1867.6.13:41–42) thus become paralectotypes.

Norman (1926) based his description of *Abramites ternetzi* on two specimens from Sao Luis and Descalvados, Mato Grosso, Brazil. The individual from Sao Luis (BMNH 1895.5.17:156) is designated as the



Fig. 6. Geographic distribution of *Abramites hypselonotus* (square = lectotype locality, filled circles = sites of other collections) and *Abramites eques* (star = approximate lectotype locality) (some symbols represent more than one collecting locality or lot of specimens).

lectotype with the second syntype (BMNH 1895.5.17:155) thus becoming a paralectotype.

Reports of *Leporinus eques* from the Paraguay basin by Boulenger (1896) followed by Eigenmann (1909) were based on the two specimens used by Norman (1926) as the syntypes of *Abramites ternetzi*. That species is herein considered conspecific with *A. hypselonotus*. *Abramites eques* has also been recorded as an element of the Rio Orinoco ichthyofauna (Fernández-Yépez 1950; Mago-Leccia 1967, 1970). Fernández-Yépez (1950:116) noted that his single specimen had 10 branched anal rays. That value falls into the range for *A. hypselonotus* rather than *A. eques*. All examined Venezuelan *Abramites* specimens are *A. hypselonotus*, and we assume that the records of *A. eques* in the Orinoco are misidentifications.

Distribution.—Río Orinoco, Río Amazonas, Río Paraguay and lower Río Paraná basins (Fig. 6).

Material examined.—BRAZIL: near mouth of River Amazon, BMNH 1926.3.2:

571, 1 (101.7, holotype of *Abramites microcephalus*). Rio Amazonas, MNHN 99-180 and 181, 2; MNHN 09-278 and 279, 2. *Pará*. Santarem, FMNH 55171, 4 (3, 39.0–43.0). *Amazonas*. Manacapuru, MCZ 21436, 9 (4, 59.3–63.8); MCZ 35348, 1. Ilha da Marchantaria, USNM 278281, 1, (60.3). Rio Solimões, Ilha Sorubim, above Coari, 10 (5, 57.6–62.9). Santo Antonio do Içá, mouth of Rio Içá, MZUSP 20998, 5 (3, 60.4–77.2). Benjamin Constant, MZUSP 20727, 3.—*Goiás*. Rio Araguaia, Ilha do Bananal, MZUSP 20673, 1 (64.7).—*Mato Grosso*. Descalvados, BMNH 1895.5.17:156, 1 (48.5, paralectotype of *Abramites ternetzi*). São Luís do Cáceres, BMNH 1895.5.17:155, 1 (54.3, lectotype of *Abramites ternetzi*; listed by Norman as being from San Luis); FMNH 55173, 2 (61.0–74.0). Santo Antônio do Leverger, Rio Cuiabá, MZUSP 4396, 1 (64.4).—*Mato Grosso do Sul*. Rio Taquari, Coxim, MZUSP 27721, 1 (88.7).

PERU: Peruvian Amazon, ANSP 21434, 1.—*Loreto*. Xeberos (=Jeberos), BMNH 1867.6.13:40, 1 (approx. 100 mm; lectotype of *Leporinus hypselonotus*); BMNH 1867.6.13:41–42, 2 (approx. 110–114 mm; paralectotypes of *Leporinus hypselonotus*). Shanso Caño, near Pebas, USNM 175915, 3 (45.7–52.6); USNM 175913, 1. Río Napo system, Cayapoza, NRM SOK/1984333.4162, 6. Iquitos, CAS 57629, 2 (86.4–112.5); USNM 167799, 3 (77.1–95.3). Río Marañon, due south of Isla Iquitos, ANSP 137814, 1. Peruvian Amazon, near Iquitos, BMNH 1977.3.10:146–149, 4. Río Yavari near Pau-mari, NRM THO/1971363.3085, 1 (78.7).—*Amazonas*. 1 km downstream from Caterpiza, LACM 41825-3, 1 (107.1). La Poza, LACM 36323-3, 1 (86.1).—*Ucayali*. Río Ucayali, Pucallpa, USNM 261479, 2 (61.4–75.2). Río Ucayali, Masisea, MZUSP 26452, 5 (2, 66.0–88.3); USNM 261491, 4 (2, 58.7–67.9); AMNH 35689, 1; AMNH 35690, 1. Río Ucayali, Utoquinia, USNM 261403, 2 (71.5–72.0).—*Pasco*. Río Picis, Puerto Bermudez, CAS 57628, 2 (101.1–108.2).

ECUADOR; *Napo-Pastaza*. Lower Río Bobonaza near Chicherota, ANSP 75958, 1 (110.8); ANSP 75957, 1 (121.4); USNM 164036, 1 (123.4); USNM 164022, 1 (92.6). Río Punino, tributary of Río Payamino, above Coca, MCZ 59420, 2 (96.8–102.8). Río Villano, USNM 164052, 2 (102.0–116.2). Río Copataza (02°00'S, 77°35'W), 2 (88.4–90.1).

BOLIVIA: *Beni*. Río Guaporé, near Costa Marquez, USNM 278282, 2 (63.0–81.6).

COLOMBIA: *Caqueta*. Río Ortegusa, near Florencia, USNM 120183, 1.—*Amazonas*. Leticia, USNM 216869, 1.—*Vaupes*. Río Vaupes, Mitu, USNM 278283, 1.—*Meta*. Río Negrito, midway between La Argelia and La Balsa, ANSP 128608, 1. Río Metica, near entrance to Lago Mozambique, ANSP 128912, 1. Río Metica, 1.5 km E of Rajote (03°56'N, 73°03'W), ANSP 128600, 1.

VENEZUELA: *Territorio Federal Delta Amacuro*. Río Orinoco (08°34'12"N, 62°15'48"W), USNM 233215, 1 (58.8). Río Orinoco, brazo Imataca, MBUCV V-13404, 1.—*Bolívar*. Río Orinoco, near Caño Arauaito, MBUCV V-13135, 1. Ciudad Bolívar, NMW 68430, 2; NMW 68429, 1.—*Guarico*. Río Portuguesa, Caño Falcon, near Camaguan, MBUCV V-9114, 2. Stream 15 km E of Calabozo, MBUCV V-04265, 1.—*Territorio Federal Amazonas*. Río Orinoco, Raudales de Ature near Puerto Ayacucho, MBUCV V-14395, 1.

PARAGUAY: “Mato Grosso or Asuncion,” CAS 57627, 1 (64.1).—*Misiones*. Río Paraná, 2 km E of Ayolas, UMMZ 207433, 4 (2, 47.1–54.9).—*Itapúa*. Río Paraná, 11.9 km E of Puerto San Rafael, UMMZ 206122, 2 (1, 96.8). Río Paraná, 1 km. E of Puerto San Rafael, UMMZ 206174, 1 (92.7).—*Concepcion*. Río Aquidaban, Paso Horqueta, UMMZ 207767, 1 (98.0).—*Presidente Hayes*. Puerto Max, FMNH 52623, 1. Río Pilcomayo, near Fortin Pilcomayo, MHNG 2226.25, 3. Villa Hayes, FMNH 55172, 3 (76.1–96.1).

ARGENTINA: *Corrientes*. San Sebas-

tian, MZUSP 10243, 1 (77.2).—*Santa Fe*. Laguna Setúbal, CIMLP 2-VIII-73-2, 6 (2, 40.0–51.0).

Abramites eques (Steindachner)

Figs. 6, 7, Table 1

Leporinus eques Steindachner, 1878:56, pl. 10, figs. 2 and 2a; type locality: Colombia, Río Magdalena.—Eigenmann and Eigenmann, 1891:51, citation.—Eigenmann 1910:426, citation, in part.—Borodin, 1929:287, aligned with *Leporinus hypselonotus* Günther.—not Boulenger, 1896: 34, Descalvados and San Luis, (=São Luís), Matto (=Mato) Grosso.—Not Eigenmann, 1909:344, Paraguay and Amazon basins.

Abramites eques, Eigenmann, 1920a:31, lower (Río) Magdalena.—Eigenmann, 1920b:16, Río Magdalena basin.—Eigenmann, 1923:117, literature compilation, Boulenger record of species in La Plata system questioned.—Norman, 1926:93, in key.—Miles, 1947:140, presence in Río Magdalena system questioned.—Dahl, 1971:111, presence in Río Magdalena confirmed.—Fowler, 1975:107, citation.—Géry, 1977:175, in key.—not Fernández-Yépez, 1950:116, Mago-Leccia, 1970:75, citation of species for Venezuela.

Diagnosis.—The possession of 13 or 14 branched anal-fin rays and five bars on the body under and posterior of the dorsal-fin distinguishes *Abramites eques* from *A. hypselonotus*, which has 10 to 12 branched anal-rays and eight body bars distributed across the body. The two species also differ in the relative lengths of the postorbital portion of the head and interorbital width (Table 1).

Description.—Morphometrics of the lectotype and paralectotypes of the species given in Table 1. Body compressed laterally, moderately deep. Greatest body depth at origin of dorsal fin. Dorsal profile of head somewhat concave above orbit. Dorsal profile of body slightly convex from rear of head

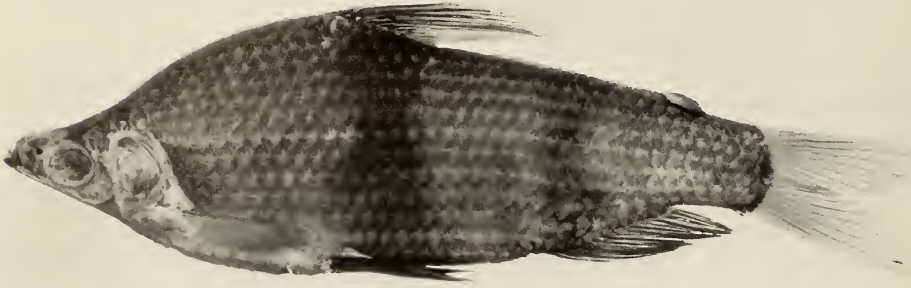


Fig. 7. *Abramites eques*, lectotype, NMW 69549, 138.8 mm SL; Colombia, Rio Magdalena.

to insertion of dorsal-fin, posteroventrally slanted at base of dorsal-fin, very slightly convex from rear of fin to caudal peduncle. Predorsal region with obtuse median ridge. Ventral profile of head straight. Ventral profile of body smoothly curved to caudal peduncle. Prepelvic region obtusely rounded; postpelvic region with median keel terminating posteriorly at anus.

Head pointed in profile, interorbital region convex. Lower jaw slightly longer than upper. Anterior and posterior nostrils of each side distinctly separated, anterior tubular, posterior elongate.

Lower jaw with four teeth on each side. Two medial teeth with inner surfaces spoon-shaped with two primary cusps, medial cusp larger with small central notch. Third tooth smaller with cusps less distinct, subequal. Lateral tooth small, with nearly straight distal margin. Premaxilla with three teeth in graded series; inner surfaces spoon-shaped. Margins of two medial teeth of each side notched, less so in smaller individuals. Lateral tooth smaller, with central notch in otherwise straight distal margin; notch absent or less apparent in smaller specimens. No teeth on maxilla. Gill membranes tightly attached to urohyal.

Scales cycloid, firm. Pored lateral line scales between supracleithrum and hypural

joint 35 or 36 [36]; 4 to 6 pored lateral line scales extending beyond hypural joint onto base of caudal-fin; canals in lateral line scales straight. Scales in transverse series from lateral line to insertion of dorsal fin $6\frac{1}{2}$ or 7 [7]. Scales in transverse series from lateral line to origin of anal fin $5\frac{1}{2}$ to $6\frac{1}{2}$ [$5\frac{1}{2}$].

Rayed dorsal-fin obtusely pointed, last unbranched and first and second branched rays longest. Dorsal-fin rays iii, 10 (first unbranched ray very short) [iii, 10]. Adipose fin of moderate size, unscaled. Anal-fin margin somewhat convex. Anal-fin rays iii, 13–14 (first unbranched ray very short) [iii, 13]. Pectoral fin obtusely pointed, extending nearly to vertical through insertion of pelvic fin. Pectoral-fin rays 14 [14]. Pelvic fin obtusely pointed, extending approximately two-thirds distance to anus. Pelvic-fin rays i, 8 [i, 8]. Caudal fin forked, unscaled. Principal caudal-fin rays 10+9.

Vertebrae 38 (2) [38].

Coloration in preservative. — Overall ground coloration of preserved specimens dark tan. Lips darkly pigmented; pigmentation continuing posteriorly as an obscure band to anterior margin of orbit. Body with five vertical, irregularly shaped bars. First bar dark, extending from base of dorsal-fin to midventral region immediately posterior of pelvic-fin insertion; posterior margin of

bar concave. Second bar very faint, extending from region posterior of dorsal fin to area anterior of anus. Third bar darker, running from middorsal portion of body to anterior anal-fin rays; anterior and posterior margins of bars concave. Fourth bar extending from anterior of adipose fin to posterior rays of anal fin. Fifth bar covering posterior portion of caudal peduncle. Dorsal fin with anterior rays and basal portion of remaining rays darkly pigmented. Adipose dorsal fin darkly pigmented along margins. Anal and pelvic fins very dark. Pectoral and caudal fins hyaline.

Common names. — Colombia: Totumito, Bonito (Dahl 1971).

Remarks. — The original Steindachner description of *Leporinus* (= *Abramites*) *eques* was based on four specimens from an unspecified locality in the Rio Magdalena of Colombia. The specimen illustrated by Steindachner (NMW 69549, 138.8 mm SL) is designated as the lectotype and the remaining individuals (NMW 69548.1, 69548.2, 69550) thus become paralectotypes.

Although *Abramites eques* was described over a century ago, we have only been able to locate the original syntypic series of four specimens in systematic collections. Eigenmann (1923:117) and Miles (1947:140) both noted that they had been unsuccessful in their attempts to secure additional specimens, with the latter going so far as to suggest that Steindachner's specimens did not originate in the Rio Magdalena system. Dahl (1971:111) noted that the species is actually quite common in a series of localities in the Magdalena basin. The illustration of *A. eques* in Dahl differs in numerous characters from the syntypes, particularly in the overall head and body forms and in the distribution of dark pigmentation on the body and on the dorsal, pelvic and anal fins.

Boulenger (1896:34) reported *Leporinus eques* from two localities in the upper Rio Paraguay basin in Brazil. Eigenmann (1923:117) questioned this identification, and

Norman (1926:93) designated that material as the type series of *Abramites ternetzi*. An examination of the two specimens (BMNH 1895.5.17:155–156) has shown they are *A. hypselonotus* (see "Remarks" under that species). The more recent citation of *A. eques* from Venezuela (Mago-Leccia 1967, 1970) has not been confirmed by available specimens of the genus from that country.

Distribution. — Río Magdalena basin (Fig. 6).

Material examined. — COLOMBIA. Río Magdalena, NMW 69549, 1 (138.8, lectotype of *Leporinus eques*); NMW 69548.1–2, 2 (118.7–163.7, paralectotypes of *Leporinus eques*); NMW 69550, 1 (106.7, paralectotype of *Leporinus eques*).

Resumen. — El género *Abramites* Fowler (1906) de la familia Anostomidae es revisado y dos especies son reconocidas. *Abramites hypselonotus* (Günther, 1868) se encuentra ampliamente distribuida en las cuencas de los ríos Orinoco y Amazonas, además de los ríos Paraguay y Paraná del sistema de La Plata. *Abramites eques* (Steindachner, 1878) se encuentra restringida a la cuenca del río Magdalena en Colombia. Las dos especies se distinguen por tener patrones de coloración y caracteres merísticos particulares. *Leporinus solarii* Holmberg (1887), *Abramites microcephalus* Norman (1926), *Abramites ternetzi* Norman (1926) y *Leporinus nigripinnis* Meinken (1935), son colocados como sinónimos de *Abramites hypselonotus* (Günther). Una clave para diferenciar las especies de *Abramites* es propuesta.

Acknowledgments

We are indebted to the following individuals and institutions for the loan and exchange of specimens, information and other assistance: Dr. Gareth Nelson and Ms. Norma Feinberg (AMNH); Dr. Barry Chernoff and Mr. William Saul (ANSP); Mr. Alwyne Wheeler and Ms. Bernice Brewster (BMNH); Dr. William Eschmeyer and Mr. David Catania (CAS); Drs. Amalia Miguelarena and

Jorge Casciotta (CIMLP); Dr. Robert Johnson and Ms. Terry Grande (FMNH); Dr. Camm Swift and Mr. Jeffrey Seigel (LACM); Dr. Antonio Machado-Allison (MBUCV); Mr. Karsten Hartel (MCZ); Dr. Marie-Louise Bauchot and Ms. Martine Desoutter (MNHN); Dr. Volker Mahnert (MHNG); Dr. Naércio A. Menezes (MZUSP); Dr. Sven Kullander and Mr. E. Ahlander (NRM); Mr. Harald Ahnelt (NMW); Dr. William Fink and Mr. Douglas Nelson (UMMZ); Sr. Hernán Ortega (Universidad Nacional Mayor do San Marcos, Lima, Peru) and Sr. Geraldo Mendes dos Santos (Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil). Figures 2 to 5 and 7 were prepared by Mr. Theophilus Britt Griswald. The Spanish translation of the "Resumen" was provided by Dr. Antonio Machado-Allison. This paper benefited from the comments and suggestions of Dr. Stanley H. Weitzman and Dr. Wayne C. Starnes. Research associated with this project was partially supported by the I.E.S.P. Neotropical Lowland Research Program of the Smithsonian Institution.

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Department of Vertebrate Zoology (Fishes), National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.